DEVELOPMENT OF SONG IN HAND-REARED BLACK-CAPPED CHICKADEES

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ABSTRACT.—Black-capped Chickadees (*Parus atricapillus*) sing a two-note tonal song that has stereotyped frequency parameters (glissando and frequency interval). We hand-reared and tutored pairs of nestlings in acoustic isolation to determine the extent that learning is involved in the production of these parameters. Each pair of birds was tutored with a high frequency *fee-bee* song, a low frequency *fee-bee* song, or a low frequency *fee* only. Song gradually developed from a warbling subsong to sustained, whistled notes. Individuals did not match the absolute frequency of their tutor songs and sang over as wide a range of frequencies as adult males do in the wild. Five of the 10 males incorporated some normal frequency parameters of the tutor songs into their own songs. None of the birds tutored with only *fee* sang with a normal frequency interval, even though they did sing songs with more than one note. Males tutored with each of the other two songs did learn to sing with the correct interval. Our results suggest that the structure of Black-capped Chickadee song is open to environmental influences and that chickadees may learn the relative frequency parameters of their song. *Received 31 July 1992, accepted 1 April 1993.*

Adult Black-capped Chickadee (*Parus atricapillus*) song is stereotyped, consisting of two pure tonal notes, onomatopoeically termed *fee-bee* (Ficken et al. 1978). Frequency descends within the first note (glissando), and there is a drop in frequency between the two notes (frequency interval). Both the glissando and the frequency interval (described as frequency ratios) exhibit very little variation among and within birds in the wild (Weisman et al. 1990). Although chickadees may shift their songs over a wide range of absolute frequencies (Horn et al. 1992), these relative frequency parameters remain remarkably stable (Weisman et al. 1990). These parameters also seem to be important for song recognition in this species (Weisman and Ratcliffe 1989, Shackleton et al. 1992).

There is some evidence that learning is involved in the development of the *fee-bee* song. Juvenile Black-capped Chickadees begin producing song during their first summer, before family flocks disperse. Often, these songs are incomplete (Ficken et al. 1978) or hoarse and imperfect (Odum 1942). Juveniles in the wild sometimes produce song where the relative frequency measures described above (glissando and frequency interval) deviate considerably from those of adult males. Often, there is no change in frequency between the notes (i.e., interval = 1.0) or the change in frequency is much larger than normal (Ratcliffe and Shackleton, pers. obs.). Nestlings reared in the absence of tutors have not been observed

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to sing normal *fee-bee* songs. These birds produce tonal sounds, but not the stereotyped song heard in the wild. Moreover, birds reared in isolation from both tutors and conspecifics do not produce any tonal sounds (Nowicki, pers. comm.).

Our purpose in this study was to determine the extent that learning is involved in the development of the relative and absolute frequency features of Black-capped Chickadee song. Specifically, we wanted to test whether birds learn the relative frequency parameters (glissando and frequency interval) of their songs, as well as whether they learn to sing at many different absolute frequencies or have the innate ability to shift the song up and down in frequency.

METHODS

We removed 21 Black-capped Chickadee nestlings from three nests at the Queen's Univ. Biological Station, Chaffey's Locks, Ontario on 8 June 1990 at 10 to 12 days after hatching (Environment Canada Permit EC0619). The day of removal is termed day 0, with respect to all other procedures reported here (normal fledging age is 16 days). The nestlings were grouped by clutch and reared following procedures and diet adapted from Lanyon (1979). We determined the sex of the birds after the experiment by laparotomy, and only vocalizations from males were analyzed.

By day 21 (i.e., birds aged 31–33 days), 18 birds had survived and were feeding independently. We then weaned them onto an adult food mix supplemented with tofu. Individuals were assigned randomly to nine groups such that no pair consisted of two birds from the same clutch. In forming these groups, however, we placed larger birds with smaller birds in an attempt to maximize male-female pairings. For the remainder of the experiment, each pair was isolated from all other birds in acoustic chambers. Sound suppression in these chambers was greater than 40 dB over the range of 2 to 12 kHz (see Ratcliffe and Weisman 1987).

We exposed the birds to a long day photoperiod (15L:9D) from day 0 until day 98. Daylength was then gradually reduced to, and maintained at, 8L:16D until day 189, then gradually increased to 15L:9D by day 214 to simulate winter and spring changes in photoperiod. Each of the nine pairs of birds was randomly assigned without replacement to one of three different training songs, i.e. three pairs of birds were trained with each song. The tutor songs were synthesized on a computer using the MITSYN sound synthesis package (Bregman 1982). The relative frequency parameters of the tutor songs were set at the species' mean values (see Weisman et al. 1990). The songs were 8-bit digitized and stored in the RAM of a Macintosh computer. We programmed a basic computer board to both command the Macintosh computer to play the tutor songs and to operate electronic switches to send these songs to the appropriate chambers. Songs were played through a Realistic Minimus-7 speaker placed in the corner of each chamber at approximately 55 dB (at 1 m; 0.0002 dynes/cm², Realistic sound level meter).

Training was carried out from day 21 to day 107 (29 June–23 September), since wild adult males sing during this period. Each morning, tutor songs were played for 60 min. at a rate of 8 songs/min. as soon as the chamber lights came on. Throughout the rest of the light period, there was a 25% chance every 30 min. that 5 to 25 songs would be played. We designed this training protocol to simulate the dawn chorus and sporadic singing throughout the day that young birds would be exposed to in the wild.

Three pairs of birds were tutored with a complete *fee-bee* song at a high frequency (group

A; *bee* = 3.30 kHz); another three pairs were tutored with a song of low frequency (group B; *bee* = 2.84 kHz). Both of these songs are within the typical frequency range in the wild, one in the upper 25th percentile and the other in the lower 25th percentile (Horn et al. 1992). The final three pairs of birds (group C) were tutored with song consisting only of the first note (*fee*) of song B. We tutored each bird with only one of these songs. Birds were kept in pairs during training in order to provide some social contact during this phase of the experiment.

During the training period, we recorded all birds once per week, for about 7 h each. On day 178, after the training period, we split up the pairs and isolated each bird in its own acoustic chamber. This was done in case singing was inhibited in the close presence of a conspecific. We recorded the birds once per week again from day 178 until day 230, that is, during the simulated spring photoperiod. We made recordings by placing an Audio-technica Pro 2ax microphone inside the acoustic chamber and recorded vocalizations on a Uher 4200 report monitor equipped with a Uher Akustomat F 413 voice activation unit. This method allowed us to record all of the birds' vocalizations, but not the intervening periods of silence. We analyzed all recordings and produced sonagrams using a Kay Ele-metrics DSP Sonagraph (Model 5500). Songs were 16-bit digitized at a rate of 20 kHz, and we used a transform size of 1024 pts. to measure frequency. Frequencies of the songs were measured at the midpoint of the last note in the song and were compared to the frequency at the midpoint of the last note (*bee*) in their tutor songs.

RESULTS

Ten of the 18 tutored birds were male. Three were trained with song A, three with song B and four with song C. Only vocalizations from these males are described here. All of the birds developed normal chickadee and gargle calls (as described by Ficken et al. 1978; also see Clemmons and Howitz 1991). Nine of the 10 males sang songs which contained elements similar to those of their tutor songs; however, only one of these birds sang a perfect *fee-bee*. Eight of 10 males were tutored in the presence of a female. The one bird that did not sing (bird A-3) was from the sole male-male pair.

Song development.—The pattern of song development was similar for all birds (sonagrams shown in Shackleton 1991). Birds first produced a warbling subsong that varied in frequency, duration, number of notes, and note structure both within and among individuals. Gradually, the warbling notes were sung less often, and more sustained tonal notes were produced. By day 110, the nine birds were singing more consistently. Although there was still variation in note number and frequency, only a limited number of note types were produced by each male. By day 178, songs of these nine birds had crystallized into a limited number of song types (Fig. 1) that did not change in structure over the remainder of the experiment. The remaining bird (A-3) did not produce crystallized songs.

Absolute frequency.—The birds did not appear to match the absolute frequency of their tutor song. A series of one sample *t*-tests showed that only four of the nine birds (A-1, A-2, B-1, and C-3) sang at frequencies
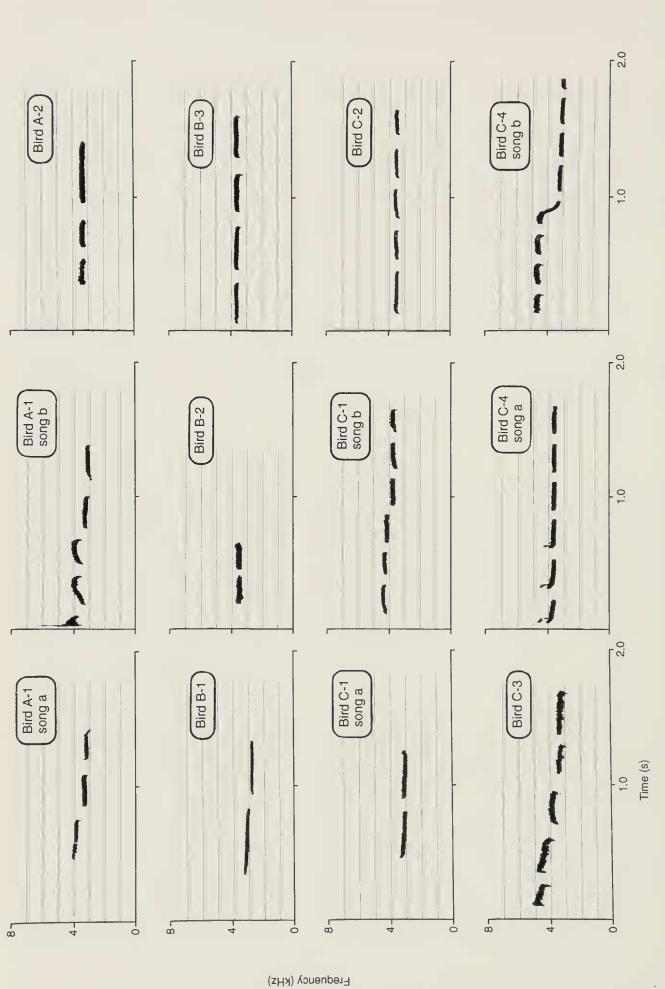
FIG. 1.   Crystallized songs of 10 hand-reared Black-capped Chickadees. Upper case letters indicate the group in which the bird was tutored, and lower case letters denote multiple song-types from the same individual.

TABLE 1

A COMPARISON OF THE FREQUENCY OF BIRDS' SONGS TO THE FREQUENCY OF THEIR TUTOR
SONGS USING A SERIES OF ONE-TAILED *T*-TESTS[a]

Bird	Mean ± SE	CV[b]	Tutor song	*t*	N[c]	*P*
A-1	3433 (± 28)	6.0	3300	0.643	53	0.52
A-2	3341 (± 12)	3.7	3300	0.338	107	0.74
B-1	2896 (± 5)	1.8	2840	1.075	131	0.29
B-2	3462 (± 22)	3.7	2840	4.838	33	0.0001
B-3	3634 (± 4)	1.0	2840	22.753	92	0.0001
C-1	3273 (± 34)	5.8	2840	2.256	31	0.03
C-2	3566 (± 14)	2.9	2840	6.938	54	0.0001
C-3	3738 (± 94)	16.0	2840	1.486	39	0.15
C-4	3736 (± 53)	11.3	2840	2.256	65	0.04

[a] Frequency values are in Hz.
[b] CV = SD/mean × 100.
[c] N = number of songs.

that were not significantly different from that of their tutor songs (Table
1). Moreover, birds tutored with song A (high *fee-bee*) did not sing at
higher frequencies than those tutored with song B (low *fee-bee*; one-tailed
t-test, $t = -0.472$, df = 4, $P = 0.33$). We also compared the ranges of
song frequencies between the hand-reared birds and 10 adult birds from
the same population recorded in the wild (Shackleton 1991). There was
no significant difference between the groups (one-tail *t*-test, $t = -1.225$,
df = 17, $P = 0.12$). The hand-reared nestlings shifted their songs over as
wide a range of frequencies as do birds in the wild and did not match the
frequency of their tutor songs. One bird, however, did match the frequency
of its tutor very closely. This bird (B-1) was also the only bird that learned
to sing a completely normal song (Fig. 1).

Frequency interval. — Two birds, A-1 (song B) and B-1, learned to sing
with a normal frequency ratio between notes. The frequency interval
between the notes was almost as stereotyped as songs recorded in the wild
(CV = 2.2) and not significantly different from that of the tutor songs
(Table 2). None of the other birds consistently produced songs with fre-
quency intervals close to those of the tutor songs. Five birds produced
notes with no change in frequency between them (i.e., interval = 1.0).
Two birds, C-1 and C-3, produced songs with notes at different frequen-
cies, but neither the magnitude nor the direction of these differences were
consistent.

Glissando. — Four birds (B-1, C-1, C-2 and C-3) consistently produced
glissandos in their songs. A note was defined to contain a glissando if it
had a frequency sweep greater than 60 Hz from start to end. These four

TABLE 2
COMPARISON OF RELATIVE FREQUENCY MEASURES OF TRAINED BIRDS' SONGS COMPARED
TO THOSE OF THE TUTOR SONG

Bird	Mean ± SE	CV[a]	Tutor[b]	One-sample *t*-test		
				t	N[c]	*P*
Interval						
A-1	1.187 (± 0.006)	3.3	1.132	1.386	39	0.17
B-1	1.121 (± 0.003)	2.2	1.153	1.299	76	0.20
Glissando						
B-1	1.039 (± 0.006)	2.1	1.028	0.535	11	0.60
C-1	1.047 (± 0.003)	1.8	1.051	0.227	31	0.82
C-2	1.047 (± 0.003)	1.3	1.051	0.269	26	0.79
C-3	1.064 (± 0.006)	2.1	1.051	0.566	12	0.58

[a] CV = SD/mean × 100.
[b] Values are those of the appropriate tutor song.
[c] N = number of songs.

birds' glissandos were highly stereotyped, and did not differ significantly from those of the tutor songs (Table 2). It is interesting to note that bird C-3 produced highly stereotyped glissandos over a wide range of frequencies within the same song (see Fig. 1). That is, it shifted *fee* notes up and down in absolute frequency but maintained a consistent glissando over this range, similar to birds in the wild (Table 2). Birds A-1 and C-4 sometimes produced glissandos in their songs, but neither bird was consistent. None of the other birds produced glissandos in their songs.

DISCUSSION

The purpose of this study was to determine how learning is involved in the development of absolute and relative frequency parameters of Black-capped Chickadee song. The fact that only one bird learned to sing a perfectly normal song limits our ability to draw conclusions from this study, however, several of the results suggest where learning is important.

Most of the birds sang over as wide a range of absolute frequencies as wild males do. The birds trained with a low *fee-bee* did not sing at lower frequencies than those trained with a high one. This suggests that the ability to shift songs may develop innately. However, the one bird which modeled its tutor song almost perfectly (bird B-1) also closely matched the absolute frequency of its tutor song and did not shift its song. Clearly, to determine whether frequency shifting is learned or develops innately will require further experiments.

Five of the 10 males learned some of the relative frequency parameters

of their tutor songs. One bird each in groups A and B learned to sing normal frequency intervals between notes, whereas none of the birds tutored with song C sang with a normal interval, even though they produced songs with more than one note. This suggests that learning may be involved in the development of relative frequency parameters. Chickadees reared in isolation are reported not to produce normal *fee-bee* song, Nowicki (pers. comm.) has observed non-tutored birds producing some tonal sounds. The effects of social stimulation from other juveniles and from a live tutor versus a recording await further study.

Black-capped Chickadees produce a large repertoire of complex vocalizations. Individuals change the structure of their calls, depending upon the calls of other members of their flock (Lempriere 1990). Similarly, birds may change the frequency of their songs in response to other singing males (Shackleton 1991). Kroodsma (pers. comm.) found that Black-capped Chickadee nestlings readily learn to sing elements of Carolina Chickadee (*P. carolinensis*) song. The crystallized songs produced by hand-reared birds are much more variable than the stereotyped *fee-bees* heard in the wild (Fig. 1; Nowicki, pers. comm.). The wide range of complex vocalizations of this species may necessitate an extensive overlap of learning and production phases in song development. That is, to be able to produce highly complex "chick-a-dee" and "gargle" calls, as well as sustained, pure tones, may require extensive practice and may explain why Black-capped Chickadees sing extensively during their first year of life and sporadically during the winter as adults (Odum 1942, Ficken et al. 1978). This may explain why only one of our birds learned to sing a normal song.

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